

On the Thorax of the Blow-fly (*Musca vomitoria*).

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(PLATES I. & II.)

General Remarks and Descriptive Anatomy.

THE following observations on the structure of the thorax of the Blow-fly embody a portion of the results obtained from a series of investigations conducted by myself at different times within the last few years on the thoracic structure of insects generally, and are offered to the Society with some diffidence.

Some time ago, on attentively considering the phenomena of wing-development in that common pest of our cellars and kitchens, the Cockroach (*Blatta orientalis*), I was induced to form the opinion that there exists in the prothorax of this insect parts which, however disguised, are the true homologues of the wings on the succeeding segments. My present object, however, is to submit such evidence as appears to me to bear upon the problem of the limits of the several segments of the connate thorax of the Diptera as exemplified in the insect which gives the title to this paper. So far as I am aware, our knowledge upon this subject has been confined to the statement that, in common with the two other orders of the Lepidoptera and Hymenoptera, the thorax of the Diptera consists mainly of the central portion of the thoracic region greatly enlarged at the expense of the other two. No definite attempt though has been made to fix by any process of reasoning the boundary which separates one of these segments from the other. According to M. Audouin, referred to by Newport *, "The parts capable of demonstration in each segment are:—on the upper or dorsal surface, the *præscutum*, *scutum*, *scutellum*, and *postscutellum*; on the inferior or pectoral surface, a single piece, the *sternum*, and on the lateral, two pieces, the *episternum* and *epimeron*, on each side; in addition to which there are also two evanescent pieces, which are of considerable size in some species, but scarcely distinguishable in others. These are the *paraptera*, portions of the thorax not articulating with the

* Article "Insecta," Cyclop. of Anat. & Physiol., p. 911, where Newport summarizes from M. Audouin, Ann. d. Sci. Nat. vol. i.

sternum, but with the episternum anterior to each wing, and the *trochantin*, articulating with the epimeron and coxa of the leg—the paraptera of the prothorax being, according to Audouin, absent.”

These parts constitute the external casing of each thoracic segment exclusive of the appendages, viz. the wings and the legs, and of the internal process known as the entosternum. Of those on the dorsal surface the scutum is the most prominent piece, and to it, in the alary segments, the articulations of the wings are affixed. In front of it is the præscutum, forming the anterior boundary of the segment, and generally bent downwards to form the horny partitions between the segments known as the phragmata. Following the scutum is the scutellum, a prominent portion of the thoracic skeleton, to which also, in conjunction with the scutum, the membranous portions of the wings (the alulets of the Diptera and Dyticidæ) are attached. Lastly, we have the postscutellum, which, like the præscutum, is generally bent downwards to form the phragma. These four pieces were regarded by Audouin* as the dorsal portions of four subsegments or annuli, of which the pectoral portions are less easily demonstrable on account of their being frequently confluent and not nearly so greatly developed. The parts forming the pectoral surface have been already sufficiently alluded to for my present purpose in the quotation from Newport. Although I cannot indorse the whole series of relations thus indicated by Audouin, and typically exemplified in the structure of the Dyticidæ, the general correctness of his views is evidenced to my mind by the fact that on those chief points which separated him from Macleay †, Burmeister ‡, Westwood §, and Newport ||, to which I shall again have occasion to refer, I find the interpretation which Audouin has put upon these questions the more consonant with my own.

Where the separation of the three thoracic segments is distinct, as, for instance, in the Coleoptera, the determination of the limits of each is a matter of little difficulty. Where, however, on the contrary, they are more or less connate, as in the Hymenoptera, and especially in the Diptera, the difficulty is proportionally increased. In the former case this is illustrated by the fact of the dispute which raged over the question as to whether the piece

* Ann. d. Sci. Nat. tom. i. p. 118 (1824.)

† Zoological Journal, vol. v.

‡ ‘Manual of Entomology,’ translated by W. E. Shuckard.

§ Introduction, vol. ii.

|| *Op. cit.*

called by Kirby * the collar was a portion of the prothorax or of the mesothorax, a question which is, I believe, generally now regarded as settled in the former sense. The different plates of which the thorax is composed can be conveniently studied by viewing them in their different aspects as seen from a dorsal, ventral, or lateral, an anterior or a posterior point of view, as the case may be. Let us first look at the thorax from an anterior point of view, as seen on removal of the head. Surrounding the cephalothoracic foramen on the dorsal surface is a slightly thickened margin, the tergum of the prothorax (Burmeister's pronotum †). A pair of rami project from it. On either side of this are two small plates, bounded inferiorly by the coxa and posteriorly by the anterior thoracic spiracle; these are the lateral plates of the prothorax, Audouin's episterna. The cephalothoracic foramen is bounded inferiorly by two plates, which Mr. Lowne ‡ has called condyles, regarding them as parts of the last subsegment of the head. From this opinion, however, I must dissent, as I shall have occasion hereafter to show §. Between the condyles is a small plate forming a peculiar organ, which he has called the cephalo-sternum, also looked upon by him as parts of the last cephalic subsegment. All these parts are indicated in my figure 5, Pl. I. Let us now turn to the dorsal surface. Here we find at its anterior angles two prominent portions, which in many species are somewhat lighter in colour than the surrounding integument; they are not marked off by distinct sutures, but their extent is sufficiently indicated by their colour and their protuberance. Burmeister (*op. cit.*) gives them the name of humeri, and says they are the same as his pronotum ||. Lowne apparently does not notice them, or regards them as part of the mesonotum; for, speaking of the anterior spiracle, he says (*l. c.* p. 72), "The mesothoracic tergum reaches over its superior margin and joins the prothorax in front of the spiracle."

It will be evident from a consideration of my figure 6, Pl. I.,

* 'Introd. to Entomology,' vol. iii. p. 548.

† Burmeister's terms, pro-, meso-, and metanotum, as applied to the entire dorsal surface of the respective segments, appear to supply a defect in Audouin's nomenclature, and will be used in the course of this paper as occasion requires, as also their opposites, viz. pro-, meso-, and metasternum.

‡ B. T. Lowne, 'The Anatomy of the Blow-fly' (Lond. 1870).

§ *Postea*, p. 28.

|| Shuckard's translation, p. 82.

that the part here referred to as overreaching the spiracle, and described as part of the mesothoracic tergum, is none other than Burmeister's humerus. I shall give reasons for thinking that Burmeister's view is the correct one*. The anterior portion of the dorsal surface is formed by a rectangular plate, the anterior angles of which are cut off by the humeri. In front it extends almost to the margin of the cephalothoracic foramen, its central portion being only separated therefrom by the narrow ring of the prothorax. Behind the humeri it extends the whole breadth of the dorsal surface, and is bounded behind by a straight transverse suture just in front of the articulation of the wings. From the circumstance that this piece is distinctly marked off from the following portion by a very evident external furrow and internal ridge, and, moreover, from the fact that it lies wholly in front of the articulation of the wings, I believe that it is the homologue of that part which in the Coleoptera especially is seen to occupy a similar position, viz. the præscutum, though in this order, as illustrated chiefly in the metathorax, it is bent inward to form the mesophragma. Following the præscutum is the large dorsal plate, the scutum, to which, as in all other insects, the wings are attached; and this is again followed by the prominent and subtriangular scutellum, to which belong the alulets. These parts are shown in my figure 1, Plate I.

We will now look at the thorax from a lateral point of view as illustrated in Plate I. fig. 6. We here notice first the parts already mentioned, and in addition the following, viz. first, the anterior spiracle immediately behind the humerus, which is followed by a large subquadrangular plate, bounded in front by the spiracle, above by the præscutum, beneath by the sternum, and behind by a smaller plate to be presently described. Mr. Lowne (*l. c.*) has called this piece the episternum; but although its relation to the sternum would seem to justify this appellation, there are yet circumstances which seem to me decidedly to remove it from the piece so designated by Audouin. It will be noticed that, like the præscutum, it is wholly and entirely anterior to the wing-socket, the latter being situate behind its superior posterior angle; and in this important respect it differs entirely from the piece which in all the Coleoptera I have been enabled to identify with Audouin's episternum. It appears to me probable that this plate is

* *Postea*, p. 22.

M. Audouin's parapteron rather than his episternum. A similar difficulty attends the identification of corresponding portions of the thoracic casing of the Lepidoptera and Hymenoptera, whose conformation in many other respects runs somewhat parallel. Behind this comes a succession of two or three smaller pieces, extending beneath the wing, and perhaps doubtfully distinct from each other. The first of these only requires special notice, as it is this piece which I look upon as Audouin's episternum. It will be seen that it, too, may justly dispute the title with the piece in front of it, while its situation *under* the wing brings it more into harmony with the piece described by Audouin under the same name, and by Chabrier* under that of "clavicule scutellaire" in the mesothorax and "plaque fulcrale" in the metathorax respectively, the anterior superior angle running up in a point under the wing-socket, which I regard as Chabrier's "appui de l'aile." The remaining pieces of the series extend between the alulet and the posterior spiracle. Their precise relations I can say little about, save that, in common with other parts forming the posterior surface of the thorax, I purpose to show that they belong to the meso- and not to the metathorax; the last of them is Lowne's lateral plate of the metathorax. There yet remain two pieces seen in profile, viz. the sterna of the meso- and metathoracic segments, as they are regarded by Lowne. This designation is unquestionably correct as regards the first, which is a large rectangular plate forming the greater portion of the ventral surface, and marked by a groove in the mesial line; but with respect to the second I shall give reasons for thinking that this also is mesothoracic and not metathoracic†. It will be observed here that it is bounded superiorly by the posterior spiracle, where it is broadest. Towards the mesial line it is much contracted, and passes between the intermediate and posterior coxæ; a portion of its anterior border also abuts upon the sternum and another upon the episternum. The parts visible on the ventral aspect have been already mostly described. In front are seen the humeri, and between them the condyles of Lowne; then follow the anterior spiracles, the episterna of Lowne (query, Audouin's paraptera?); and between them the large sternum of the mesothorax, followed by the acetabula and coxæ of the intermediate and posterior legs; and on either side of these are

* See Chabrier, "Essai sur le Vol des Insectes," Mémoires du Muséum d'Histoire Naturelle.

† *Postea*, p. 27.

the posterior spiracles, the plates between them and the wings, and Lowne's metathoracic sternum (?). One portion, however, has not yet engaged our attention, viz. the narrow plate between the acetabula of the anterior coxæ. This is called by Mr. Lowne the prosternum. He says* :—" It consists of a central portion and two cornua. The central portion is a long narrow plate widest anteriorly ; it is grooved along the mesial line externally, and presents a slight ridge internally ; posteriorly it sends a narrow plate along the edge of the mesosternum and between it and the posterior edges of the coxæ on either side. This plate becomes broader externally to the coxa, and extends along the outer edge of its articulation, reaching the lower anterior margin of the anterior spiracle, where it unites with the lateral plate of the prothorax, and terminates in a curved point in front of the articulation of the coxa near its outer anterior angle behind the condyle."

The description appears mainly correct, though I shall have occasion to differ from it in two particulars—first, the dissociation of the condyles from the central carina between the coxa, owing to their allocation in the " fifth or last cephalic segment" † ; and, secondly, the association therewith of the cornua, by which I understand the narrow plate which, as stated, runs along the edge of the mesosternum, and which I believe to be Audouin's epimeron ‡.

Lastly, we will look at the thorax from behind, having first carefully removed the abdomen. Some of the parts already referred to appear again. Above is seen the scutellum, on either side the posterior spiracles with the plates surrounding them, and beneath are the coxæ. In addition to these we have the two capitulate organs called halteres, which, as I shall show, take the place of the posterior wings and a large surface of integument lying between them, separated superiorly by a narrow membranous conjunctiva from the scutellum, and having an emarginate contour beneath to allow a passage to the viscera. A semilunar space intervenes between its inferior margin and the lateral plates forming Lowne's metasternum, into which project two slender apodemes connected with the halteres. About the centre of its length runs the junction of the first abdominal segment with the thorax, which extends between the bases of the halteres and

* Anatomy of the Blow-fly, p. 63.

† *Postea*, p. 28.

‡ *Postea*, p. 27 (footnote).

separates the superior or external portion from the inferior or internal.

The whole of this large surface forms Lowne's metathoracic tergum*, so that, according to his view, we have the whole of the pieces surrounding the thoracic abdominal foramen metathoracic, viz. the metathoracic tergum and the lateral and sternal plates of the same segment. That the same opinion was held by Burmeister appears from the fact that he recognizes the same plate between the coxæ as the metasternum†; and his figures on pl. xiv. of the thorax of *Tabanus bovinus* and *Myopa testacea* afford similar evidence. In assigning these plates, therefore, to the mesothorax, I am conscious that I shall differ from a weight of authority. With respect to the posterior spiracles also, I must differ from Westwood‡ in assigning them too to the mesothorax instead of to the metathorax, whilst agreeing with him in regarding the halteres as appendages of the latter segment, in opposition to Audouin and Latreille, who looked upon them as abdominal.

So much for the external integument of the thorax. We must now shortly notice the internal processes which form the entosterna of the several segments. In the first place, we find the pair which are found at the posterior extremity of the prosternum and reach the lower margin of the anterior spiracles; they are referred to by Lowne§, and form, I believe, the prothoracic entosternum||. Similar horny rami arise from the extremity of the sternum in many Coleoptera: for example, in the mesothorax of *Geotrupes stercorarius*, *Dyticus marginalis*, and *Rhizotrogus solstitialis*. The mesothoracic entosternum extends the whole length of the sternal piece as a thin triangular vertical plate, with a pair of lateral processes for the insertion of muscles. The entosternum of the metathorax arises between the posterior coxæ and is much narrower. A projecting point of integument between them represents the whole breadth of Lowne's metasternum (my mesothoracic epimeron) in the mesial line.

Now in deciding the question as to which segment any one of the parts here described belongs, we may be guided by three considerations:—

1st. The analogy presented by other insects:

* Anatomy of the Blow-fly, p. 65.

† Shuckard's translation, p. 85.

‡ Westwood's Introduction, p. 500.

§ *Op. cit.* p. 63.

|| *Postea*, p. 28.

- 2nd. The evidence derivable from developmental change ;
 3rd. That obtainable from a consideration of the nervous and muscular systems.

Considerations of Analogies in divers Insects.—I may observe that the three orders of hexapod insects associated by Packard* under the name of Metabola, viz. the Lepidoptera, the Hymenoptera, and the Diptera, beside the point of resemblance pointed out by him, have this in common, viz. the excessive development of the mesothorax at the expense of the preceding and following segments. That this is broadly the case is, I believe, an admitted fact irrespective of questions at present under discussion ; and it will be worth our while to consider what relation this preponderance of the mesothoracic over at least the metathoracic region bears to the development of the wings and to their effectiveness as organs of flight. Of the three orders it may be said that the Lepidoptera is that in which the size and effectiveness of the posterior wings are most nearly approximated to that of the anterior †. The posterior wings of the Hymenoptera are decidedly inferior to the anterior in size ; and it may perhaps be presumed that their efficiency as organs of flight is subordinate to and dependent upon the former, whose movements they are evidently formed to follow. Lastly, in the Diptera, the posterior wings are only found under the guise of halteres, and for purposes of flight are entirely obsolete.

Thus in these three orders we are brought, by a succession of stages, from a condition in which the size and effectiveness of the wings are somewhat equal, to one in which the posterior are atrophied, and the power of flight is entirely concentrated in the mesothorax. Let us see if we can trace a similar succession in the development of the segments themselves. If we can succeed in showing that the comparative development of the two alary segments in the Lepidoptera and the Hymenoptera is in proportion to their wing-power, as I may term it, we shall then have an *à priori* ground for thinking that the comparative development of the segments of the Diptera follows the same rule ; in fact, that the metathorax is almost as obsolete as the wings, and that nearly the whole of the thoracic region is mesothoracic.

* Guide to the Study of Insects, p. 104.

† From the absence of longitudinal dorsal muscles in the metathorax of the Lepidoptera, I incline to the opinion that even in this order the posterior wings are subordinate to the anterior.

But in order to do this we must first decide any disputed questions that may arise as to the limits of the thorax in these two orders. I believe that as regards the Lepidoptera there is no dispute as to the limits of the metathorax. In *Liparis salicis* (Pl. II. fig. 9), behind the lozenge-shaped scutellum of the mesothorax, we find the metathoracic scutum visible as a triangular space on each side, the mesothoracic postscutellum and the metathoracic præscutum both being developed inwardly; this is followed by a minute scutellum and postscutellum, the latter also developed inwardly. Thus it will be seen that though of considerably less extent than the preceding segment, the metathorax has still a very appreciable breadth to correspond with its wing-development. Turn we now to the Hymenoptera. Here we are at once met with an old and hotly-disputed controversy. Audouin* and Latreille* believed that the posterior portion of the thorax in this order is not strictly thoracic—that is, that a portion of the fifth segment of the body entered into its composition; while Macleay† was of opinion that the said portion was the scutellum of the metathorax enormously enlarged; and Westwood‡ seems also to have regarded it as thoracic§. I do not know that this question is regarded as settled even now, although the view taken by Packard|| is, so far as concerns the Hymenoptera, similar to Audouin's and my own; and I think the balance of opinion inclines that way¶. It will be evident, however, on a little consideration that the decision of this question must largely affect the course of our reasoning, for if we adopt Macleay's views we shall have in the Hymenoptera a metathoracic development out of proportion to that of the posterior wings. I will therefore advance a few arguments to show that in this matter Audouin and Latreille are right as opposed to Macleay; and in the first place draw attention to the two figures illustrating different stages of the development of the pupa of the

* See Westwood's 'Introduction,' vol. ii. p. 75.

† Zoological Journal, vol. v. p. 172.

‡ *Tom. cit.*

§ Burmeister and Newport were also opposed to Audouin on this point. See Shuck. Transl. Burm. p. 235, and Newport's "Insecta," Todd's Cycl. Anat. and Physiol. p. 55.

|| Packard's Guide to the Study of Insects, pp. 67 & 109.

¶ Subsequent to the reading of this paper, I have noticed that Sir John Lubbock and Dr. Ratzeburg take the same view. See abstract, "The Anatomy of Ants," Journ. Linn. Soc., Zool. (No. 80), vol. xiv. p. 738. I may also quote H. Reinhard as supporting a similar view, *vide* Berlin. entom. Zeitschr. 1865, p. 207.

Humble-Bee from Packard *. In the first of these the fifth segment of the body, the thoracico-abdominal segment of Newport, is seen to follow the alary segments and to be very similar to the succeeding abdominal ones, differing only from them in the form of its oblong spiracle, by which, however, it is easily and certainly recognized in the succeeding stage, where it is seen that the thoracic abdominal incisure has taken place behind it, including it with the thorax. If further evidence be required, I would point out that the Hymenoptera are not so exceptional in this matter as may be thought †, and that the Coleoptera, as a rule, if not also the Heteroptera, exhibit a similar structure. That the Coleoptera do so has long come under my notice; and I believe Audouin pointed out the same thing. If we look at the dorsal surface of *Rhizotrogus*, *Geotrupes*, or *Dyticus*, we find in either case the dorsal plate of a segment whose ventral arc has disappeared (the segment is ventrally atrophied). This dorsal plate is unmistakably the first of the abdominal series, and furnished, like all the succeeding ones, with a pair of spiracles, differing from the others chiefly in being larger. It is quite distinct from the metathorax, following, as it does, the inwardly developed and obtusely triangular postscutellum (see Pl. II. fig. 15, for postscutellum of *Rhizotrogus*). In default of its own ventral arc, however, it is thrown forward, as it were, upon the dorsal surface of the metathorax, or the ventral surface of that segment is produced underneath it so as to supply the place of the lost ventral arc. It is as if the great development of the ventral surface of the metathorax had absorbed that of the next segment. A like conformation, I believe, prevails in many Heteroptera. Newport ‡, I ought to add, has noticed a general atrophy of the fifth segment of the larva in insects, though he does not appear to have connected it with the ventral atrophy of that segment in the imago to which I have re-

* "On the Morphology of Insects," Proc. Boston Soc. Nat. Hist., Feb. 1866, p. 282, and the figures on p. 294.

† I cannot quite understand how it is that Packard seems to have ignored this fact; for, in the paper alluded to in the previous note, he says (p. 291), "The Hymenoptera differ from all other insects in having the basal ring of the abdomen thrown forward upon the thorax." The phenomenon is, I admit, not so strikingly marked in the two other orders as in the Hymenoptera; still it is, I venture to think, very pronounced, as I have endeavoured to show. Amongst the Heteroptera I would adduce the case of *Coreus marginatus* as the result of my own observation.

‡ Todd's Cyclopædia of Anatomy, "Insecta," p. 28.

ferred. In general the dorsal plate of the atrophied segment is about equally united with the thorax and the abdomen; but instances occur in which it approximates more closely to the former; and as this brings it nearer the structure of the Hymenoptera, I have illustrated it in the case of *Goerius olens* (Pl. II. fig. 13). It will be remarked that the metathoracic postscutellum, which is usually developed inwardly to form the metaphragma, is here raised to the surface, forming the triangular piece between the two halves of the dorsal plate of the atrophied segment, which, as usual, is furnished with a pair of spiracles, and is separated by a broad membranous conjunctiva from the first of the true abdominal series, its lateral margins being conterminous with the epimera of the ventral surface of the metathorax. Precisely the same thing has happened in the Hymenoptera, both petiolated and non-petiolated, only that in the former the thoraco-abdominal incisure being so much deeper and taking effect more on the dorsal surface, the union of the dorsal plate of the atrophied segment with the thorax becomes more striking, and therefore seems to have attracted exclusive attention.

The phenomenon is well seen in the Humble-Bee, of which I have given a drawing (Pl. II. fig. 6), where it will be seen how large a portion of the posterior surface of the thorax is occupied by this plate, reducing the metathorax in the mesial line at least to a mere ridge between it and the scutellum of the mesothorax, with a small triangular expansion on either side, to which the bases of the posterior wings are affixed. The section of the metathorax in the mesial line is shown in fig. 5, and it will at once be seen that, viewed in this light, that segment is now reduced to something like conformity with the subordinate character of its alary appendages. It might be expected that these organs, which are (in virtue of the hooklets by which they are united with the anterior pair) evidently formed to follow the movements of the latter and depend on them for their motive power, would require little or no provision of muscular force for themselves; and accordingly we find an almost atrophied metathorax and no muscles in it.

We now see therefore that in the two orders of the Lepidoptera and Hymenoptera the development of the segment is proportioned to the development of the wings. Surely, therefore, there is good *à priori* ground to expect that in the Diptera the same rule will hold independently of the reasons to be presently

adduced, and that we shall find the metathorax of this insect to be as obsolete as are the alary appendages it carries.

Let us see now how the view of the thoracic structure of the Hymenoptera thus advocated bears upon the position of the spiracles. Does it introduce an element of harmony into the study of this order as compared with other insects, or one of additional perplexity? and, finally, what is its effect on the location we may give to these organs in the Diptera? I gather from a passage in Westwood* that Latreille has made the observation that the metathorax in insects is never provided with spiracles. The observation is a good one, though not free from error, I venture to think, in the induction he draws therefrom, that they (and the halteres in consequence) are abdominal appendages. Of course, on his view of the Hymenopterous structure, they are excluded from the metathorax of that order inasmuch as, in his opinion also (as I have just mentioned), they occur on that portion of the body which belongs to the fifth or atrophied segment; and so far as I am acquainted, with the exception of the Diptera, there is no other order of insects in which a metathoracic spiracle may even be thought to be observable in the *imago*. By regarding, therefore, the posterior spiracle of the Diptera as mesothoracic, we shall introduce this element of agreement into the structure of the class—not indeed by thrusting it, as Latreille did, into the abdomen, that is, by removing it backward from the metathorax, but by the converse process of removing it forward to the mesothorax. We shall then have the metathorax in every order of insects devoid of a spiracle. That the posterior spiracle should be mesothoracic is absolutely essential to my argument, since it is surrounded by plates which I propose to show also belong to that segment.

But again, so far as I am acquainted, in every case where the limits of the thoracic segments are not subject of discussion, the position of the thoracic spiracles is, roughly speaking, between the segments, one pair between the pro- and mesothorax, and another pair between the meso- and the metathorax, though in some orders the latter are suppressed. Both pairs occur, for example, in the Coleoptera and Lepidoptera; one only in the Hymenoptera, viz. the anterior. I say roughly, because I think there is really no debatable ground between the segments, and that any

* Westwood's 'Introduction,' p. 500.

given portion of the tegumentary structures must belong to one or other of those between which it seems to occur; and it will, I think, be found that the spiracles are in every case more nearly approximated to the segment in front of them than to that behind. Indeed I have noticed that the largest tracheal branch of the spiracle between the pro- and mesothorax of *Acrida viridissima* proceeds immediately down the fore leg to that peculiar organ in the fore tibia which has been supposed to be connected with the sense of hearing.

From this and similar indications I think that the spiracle is always the property of the posterior surface of the segment in front of it. And this is an additional reason for thinking that the posterior spiracles of the Diptera are mesothoracic, viz. that they are thus made to occupy the posterior or postscutellar region of the segment to which they belong. That they should in the Blow-fly be surrounded by well-developed corneous plates instead of membranous integument, is only an indication of the general fact that the postscutellar region has participated fully as much as the other portions of the mesothorax in the exceptional development which the segment has received in this order.

Evidence from Developmental Change.—In a paper read three years ago before the Quekett Microscopical Society, "On the Metamorphosis of the Crane-fly and of the Blow-fly," I took occasion to notice the dorsal appendages on the thorax of the pupa of these insects. I believe that these processes, which are indicated in my figures (Pl. II. fig. 1 and Pl. I. fig. 13), are the proper dorsal appendages of the prothorax, corresponding on that segment to the wings on the following one. The purport of their being seems to terminate with the pupa state; and in the imago their development as appendages seems to be arrested. As I endeavoured to show on that occasion, the fact of their being the serial homologues of the wing is not only attested by their position, but by the manner of their development, arising, as they do in either case, from a special imaginal disk, which, in the Blow-fly at least, had hitherto escaped notice from its minuteness.

This disk is shown in the case of the Crane-fly (Pl. II. fig. 12), where it will be seen to correspond exactly in position to those of the wings and halteres which follow it, viz. a little outside of, and posterior to, that of the corresponding leg. The corresponding disk of the Blow-fly is situated just behind the

anterior spiracle of the larva immediately under the integument, and partially surrounding the anterior termination of the main trachea. I think that in this case similarity of development is a strong argument in favour of similarity of homological relationship; and again it may be asked, if they be not the homologues of the wings, how are we to regard them? To look upon them as abnormal productions would, I submit, be contrary to the whole spirit of philosophical inquiry; and what other opinion we can form I know not. If, then, they be the proper dorsal appendages of the prothorax of the pupa, then the imaginal structures found immediately underneath them must in all probability correspond, and be prothoracic too. But these structures are the humeri to which I have had occasion to refer. Therefore, with Burmeister, I must look upon these parts as prothoracic*, and consider them as the homologues of the posterior angles of the collar of the Hymenoptera, the homologous parts in both orders being followed immediately by the spiracle.

But it is not only in the prothorax that the observation of developmental change will afford a clue to the division of the segments. In the pupa of the Crane-fly the dorsal surfaces of the meso- and metathorax are sufficiently and distinctly marked, the former being as conspicuous for its extent as the latter for its contracted dimensions; and, strange to say, their dorsal appendages are not yet recognizable as a pair of wings and a pair of halteres, but as two pairs of undoubted wing-cases similar to each other in every respect but that of size. It is only when we separate the latter pair and examine them carefully with a lens that we can persuade ourselves that the nascent organs within them are not really wings, but the familiar halteres (see Pl. II. figs. 3 & 4). They are, so far as I judge, unquestionably modified and abortive posterior wings, appendages of a metathoracic segment, however, reduced, and by no means abdominal, as was supposed by Latreille.

Again, on carefully removing the integument from the dorsal surface of the Crane-fly pupa over the posterior portion of the mesothorax, in front of its junction with the metathorax I disclosed the plate marked *ps* in the drawing of the imago (Pl. II. fig. 2), which I must therefore regard as mesothoracic. This plate is nearly horizontal in the Crane-fly; but a compa-

* *Anteà*, p. 12.

ri-son of the two insects convinced me that it corresponds with the upper or external portion of the vertical surface which Mr. Lowne (*op. cit.*) calls the metathoracic tergum. For this reason also, therefore, I must hold this to be a mistake, and that the external portion at least of the surface in question belongs to the meso- and not to the metathorax.

As to the Muscular and Nervous Parts.—But fully as cogent as either of the foregoing considerations is the evidence to be derived from an examination of the muscular structure. The nervous system of insects presents, to some extent, the repetition of parts observable in the integument. There is generally in the larva a pair of ganglia with corresponding nerves for each segment. Owing, however, to the concentration of the nervous centres in the thorax of the imago (a concentration which, in the Diptera, is carried to an extreme point), and their consequent fusion into one large nervous mass, it is less adapted to the study of homological relations than the muscular structure. The latter, however, appears to me so obvious and so comparatively easy a means of discrimination, that any diagnosis of external relations that does not take it somewhat into account must of necessity be *pro tanto* imperfect. The subcuticular muscles of larvæ present a very uniform repetition. Each segment has its own set of muscles distinct from those preceding and following it. I will not say that such a thing never occurs as the existence of a muscle extending across two or more segments, for I know at least of one instance in which this certainly appears to be the case*; still, as a rule, observable not less in the imago than in the larva, each segment is provided with its own muscles; and the connate condition or any approximation to it of two or more segments is not, so far as I know, accompanied by any fusion, either real or apparent, of their respective muscles.

To illustrate this, it will be necessary to mention that the thoracic muscles of insects assume two different principal directions †, a longitudinal and a lateral or vertical one. The former occupy

* This occurs in the larva of the Crane-fly; and a similar instance is mentioned in Sir John Lubbock's paper "On the Muscles of the Larva of *Pygæra bucephala*" (Trans. Linn. Soc. vol. xxii. p. 174), being that marked No. 2 in the first Plate attached thereto.

† For a more complete account of the muscular structure of the thorax, see "Essai sur le Vol des Insectes," par J. Chabrier, in *Mémoires du Muséum d'histoire Naturelle*, p. 410.

the central portion of the thoracic cavity towards the dorsum, and are chiefly conspicuous in the alary segments, and (with the exception of the Libellulidæ) more especially of such insects as are remarkable for their power of flight, in the production of which, as is shown by Chabrier, they are chiefly instrumental. They fall in two divisions, one on either side of the mesial line, as may be seen in Plate I. figs. 8, 10, & 11, and in Plate II. figs. 5, 10, & 11. They extend from the præscutum to the post-scutellum of the segment to which they belong, in every insect with which I am acquainted, and are the "muscles dorsaux au abaisseurs des ailes" of Chabrier, the recti dorsales of the larva.

In the Coleoptera, where the thoracic segments are unmistakably distinct and the phragmata well developed, their attachments are equally clear; here, however, they are chiefly confined to the metathorax, as the faculty of flight in those insects resides in that segment. In *Acrida viridissima* we have an example where that faculty is resident in both segments; and accordingly we find that the longitudinal muscles are present in both (see Pl. II. fig. 11); and though the two alary segments are much more intimately united in this insect than they are in the Coleoptera, the two sets of muscles are perfectly distinct, the length of each being coextensive with the limits of the segment to which it belongs.

In the Lepidoptera the same rule holds. The anterior wings of these insects would appear to be the chief agents of flight; for we find the dorsal longitudinal muscles confined to the mesothorax, the vertical ones only being found in the succeeding segment. They extend from the præscutum to the postscutellum, from the pro- to the mesophragma, both of which partitions are well marked. See Pl. II. fig. 10, which represents a section of the thorax of *Liparis salicis*.

In the Hymenoptera a somewhat singular conformation exists, which was first, I believe, pointed out by Macleay. The mesothoracic postscutellum is detached in the mesial line from the scutellum, and only remains attached by its lateral extremities, so that the narrow rim of the metathorax follows immediately upon the scutellum of the preceding segment. Nevertheless that the detached septum thus formed is the postscutellum of the mesothorax is evidenced, as Macleay says, by the fact that when

the meso- is separated from the metathorax, it always comes away with the former. In the mesial line it projects far backwards into the posterior portion of the thoracic cavity so as to leave but little space between it and the posterior wall, which, as I have said, is formed by the dorsal plate of the fifth segment. Thus the longitudinal muscles of the mesothorax, which are the only thoracic longitudinal ones developed, pass from it to the præscutum, across the minute groove of the metathoracic tergum and the cavity of the mesothoracic scutellum, as may be seen in Plate II. fig. 5, which represents a longitudinal section in the mesial line of the thorax of the Humble-Bee. There is no fusion of the muscles of the two segments. The mass of muscles which nearly fills the united cavity of three segments belongs but to one of them, viz. the mesothorax; the metathoracic muscles, both longitudinal and vertical, being no longer required, are altogether obsolete.

Now for the application, so far as the longitudinal muscles are concerned. Plate I. fig. 8 shows the longitudinal muscles of the Blow-fly. They are seen to extend from the mesothoracic præscutum in front to that vertical posterior surface which Burmeister and Lowne regard as the metathoracic tergum, but which, I venture to submit, is again, as it has been shown to be in all previous cases, the mesothoracic postscutellum, the mesophragma, and not the metaphragma. If it be otherwise, we shall have what I can find no other instance of, viz. a commingling of the principal muscles of two segments into one homogeneous muscular mass.

Again, be it observed from Plate I. figs. 8 & 11, that although the longitudinal muscles extend in the mesial line almost to the verge of the cephalothoracic foramen, they have not sufficient breadth to reach the anterior angles where the humeri are situated. It will be obvious that if this were the case, I could no longer hold the humeri to be prothoracic; but as it is, the avoidance by the mesothoracic muscles of these portions of the integument is, I submit, significant of the correctness of my view.

Further, let us see what may be learnt from a study of the transverse or vertical muscles of the thorax, proceeding on the assumption, warranted by general observation, that none at least of the principal of these can have their origin in one segment and

their insertion in another*, and that where two segments are concerned there is sure to be more or less repetition of the muscles presented to view.

Let us glance for one moment at the muscular structure of *Aeshna grandis*. This insect is remarkable for its power of flight, and yet, contrary to the general rule, the longitudinal muscles are almost obsolete, the deficiency being made up by the number and high organization of the vertical ones. The alary segments are not very clearly separated externally, but internally an inspection of these vertical muscles shows clearly that the united cavity they occupy is formed of two segments. After removing the two principal masses which towards the mesial line are attached to the bases of the wings, and which obstruct the view of those behind, we find a number of others which have their insertions formed in a peculiar and very beautiful manner by a round plate, or "cupule" as Chabrier calls it, to the concave surface of which the muscles are attached, while from the other proceeds a tendon to the point requiring motion. These muscles, with the exception of the last, are repetitions in two sets, 1 2 3 4, 1 2 3 4 (see Pl. II. fig. 14), showing the existence of two segments.

But there is no such repetition in the vertical muscles of the

* If there be any doubt felt as to the correctness of such an assumption, let us look a little further into the matter. Passing by my own observations on the point, though the statement is founded mainly upon them, I may refer to the figures of Lyonet, in his *Anatomy of the Larva of Cossus ligniperda*, and to Sir John Lubbock, "On the Larva of *Pygarea bucephala*," Linn. Trans. vol. xxii. p. 173. Of the following corresponding lateral muscles in the two insects, viz.

α	Lyonet = 37?	and 38	Lubbock,
β	„	= 49 and 50	„
γ	„	= 46, 47, and 48	„
δ	„	= 51	„
$\zeta?$	„	= 33 and 34	„
$\theta?$	„	= 35? and 36	„
m	„	= 40	„
n	„	= 43	„

only the four marked thus (?) appear to offer a shade of doubt in this respect; and these cases are indeed, as I may say, doubtful ones. The question is not exactly whether they actually cross the border-line between the segments, but rather whether they are attached by one extremity thereto, and that, in the case of $\theta = 35$, only in a partial sense, the anterior fasciculi only being in question.

Fly, in which three principal masses are observable (Pl. I. figs. 9, 10, & 11), the anterior being the "sternali dorsaux" of Chabrier, and the posterior his "costali dorsaux"; the intermediate one I am uncertain about.

Inasmuch, therefore, as there is no repetition, the muscles, I submit, are those of one segment. Again, the central mass of vertical muscles connects the anterior portion of the mesothoracic scutum with the plate that Burmeister and Lowne call the metasternum. How can this be? There is only one answer. This plate is not, as they regard it, metathoracic*.

In addition to its muscular connexion with the mesothoracic scutum, I would suggest the following reasons for regarding it as the mesothoracic epimeron. We have seen from Mr. Lowne's account (*op. cit.*) that the prothoracic sternum sends out posterior to the coxæ two "cornua," which, passing outwards, expand into small plates that surround the acetabula of the fore legs and reach as far as the anterior spiracles (see Pl. I. fig. 2), the condyles, and the lateral plates of the prothorax. In a perfectly similar manner it appears to me that the mesothoracic epimera, if I may be allowed so to call them, originate from the posterior extremity of the sternum of that segment, and, passing outwards, surround the acetabula of the intermediate legs, and are there brought into contact with the spiracles, the sternum of the segment, and the posterior lateral plates of Lowne, Audouin's episterna. It is a character of Audouin's epimeron that it is always in connexion with the coxa, and articulates with the sternum and episternum of the segment†. Again, the posterior mass of vertical muscles, the costali dorsaux of Chabrier, unites the posterior portion of the mesothoracic scutum with Lowne's lateral plate of the metathorax just above the posterior haltere. This, too, appears inconsistent with the rule of muscular structure adverted to; and I must regard this plate also as part of the mesothorax, though I am unable to identify it certainly with any of Audouin's pieces; I think it probably forms part of the postscutellum, together with the central portion between the bases of the halteres.

Thus it appears to me that the analogy of other insects, the

* *Anteà* p. 13.

† *Cyclop. of Anat. and Physiol.*, "Insecta," p. 48, for which reason also I regard the above-mentioned cornua as the epimera of the prothorax, as stated *anteà* p. 14.

phenomena of development, and the study of the muscular system, all combine to show that the thorax of the Diptera as illustrated in this insect is almost exclusively mesothoracic. Nothing is left of the metathorax except the halteres, a narrow strip possibly along the posterior edge of the mesothoracic epimera, the coxæ, and the entosternum of the segment, to which must be added the posterior surface of the mesophragma, formed, as in many other cases, by the inversion and adherence together of the two layers of integument of the postscutellum of the one segment and the præscutum of the other. The only remnants of the metathoracic muscles which exist are two thin slips which, originating at the posterior surface of the mesophragma close to the halteres, pass downward and forward, and are inserted in the entosternum of the metathorax. The fact of their being so inserted proves that they are metathoracic muscles. The further fact of their originating on the posterior surface of the mesophragma again shows that that posterior surface is metathoracic, as just stated, and that the cavity of the metathorax, if cavity it can be called, is posterior to this surface and continuous with that of the abdomen. Again, if a further proof be sought, it may be found in the projection into that cavity of the two slender apodemes of the halteres before referred to.

Lastly, I may add a few words on the light the muscular system throws on the boundaries of the prothorax. We have seen how the longitudinal muscles of the mesothorax avoid the humeri. I would now point out, from Pl. I. figs. 9 & 11, that the vertical muscles do the same, not being sufficiently advanced anteriorly to reach them; while, on the other hand, a muscle of considerable size, which, passing as it does to the anterior coxa, must, I submit, be regarded as prothoracic, takes its origin from the same parts (see Pl. I. fig. 12). Furthermore, that the condyles form part of the prothoracic segment*, I must conclude from the observation that a pair of muscles connect their interior surfaces with the rami which represent the entosternum† at the posterior inferior margin of the segment behind the coxæ; they represent probably the anterior lateral processes of the prosternum of the Coleoptera.

I shall only further remark that truth is frequently only to be

* *Antea*, pp. 11 and 14.

† *Antea*, p. 15.

arrived at through a series of errors, and that I can scarcely hope that all my observations will prove exceptions to the general rule.

DESCRIPTION OF THE PLATES.

All the illustrations are necessarily much magnified.

The parts of the thorax are designated in accordance with my own view of their relations, except where indicated in brackets, and are lettered the same throughout the series of figures, viz. :—

h. The humerus. *prs.* The præscutum of the mesothorax.

scm. The scutum of the mesothorax.

scm'. „ „ metathorax (not found in the Blow-fly).

scl. The scutellum of the mesothorax.

scl'. „ „ metathorax (not found in the Blow-fly).

con. Lateral processes of the prosternum (Lowne's condyles).

epis. The lateral plates (episterna) of the prothorax.

sp. The anterior (prothoracic) spiracle.

sp'. The posterior (mesothoracic) spiracle.

*sp**. The spiracle of the fifth segment.

cox, cox', cox''. The anterior, intermediate, and posterior coxæ.

par. The parapteron (Lowne's anterior lateral plate of the mesothorax).

epim. The epimeron of the prothorax (Lowne's cornua).

st. The sternum of the prothorax.

st'. „ „ mesothorax.

epis'. The episternum of the mesothorax (Lowne's posterior lateral plate).

x. Uncertain (Lowne's lateral plate of the metathorax).

epim'. The epimeron of the mesothorax (Lowne's metasternum).

ps. The postscutellum of the mesothorax (in Pl. I. Lowne's dorsal plate of the metathorax).

ps'. The postscutellum of the metathorax (not found in the Blow-fly).

lm and *vm.* Longitudinal and vertical muscles of the mesothorax of the Blow-fly (Pl. I.).

mes. Mesothorax (Pl. II.); *met.* Metathorax (Pl. II.).

i. The dorsal plate of the fifth segment (Pl. II.).

m. The longitudinal muscles of the mesothorax (Pl. II.).

m'. „ „ metathorax (Pl. II.).

PLATE I.

Fig. 1. Dorsal surface of thorax of Blow-fly.

2. Ventral surface of ditto: *f*, the cephalothoracic foramen; *ac*, acetabulum of fore leg; *hal*, the haltere.

3. Entosterna of meso- and metathorax, side view.

4. The same, from above.

Fig. 5. Anterior view of prothorax; *pr*, pronotum.

6. Lateral view of thorax.
7. Posterior view of ditto: *ps*, postscutellum of the mesothorax; *mph*, mesophragma formed by the united postscutellum of the mesothorax and the præscutum of the metathorax†; *al*, alulet; *mm*, metathoracic muscles proceeding to metathoracic entosternum; *ap*, apodeme of haltere; *z*, narrow margin, probably remains of lateral plate of metathorax; *j*, line of junction of thorax and abdomen.
8. Longitudinal vertical section of thorax in the mesial line, showing longitudinal muscles: *prov*, the proventriculus followed by the chyle-stomach.
9. The same, with the longitudinal muscles removed, showing:—*vm*¹, *vm*², *vm*³, the vertical muscles; *pm*, prothoracic muscle inserted in the fore coxa; *mm*, metathoracic muscle to entosternum.
10. Transverse vertical section of thorax, showing muscles.
11. Horizontal longitudinal section of ditto.
12. Internal view of a portion of the thoracic cavity, showing:—*pm*, the muscle of the fore coxa; *m*^{*}, small muscles connected with the wing beneath the parapteron. A strong process, *g*, of the præscutum is seen to bridge across the humerus without touching it.
13. The pupa of the Blow-fly: *o*, the compound eyes; *pa*, the prothoracic dorsal appendages.

PLATE II.

Fig. 1. Pupa of Crane-fly. Anterior portion, showing:—*pa*, the prothoracic appendages; *mes*, the posterior portion of the mesothorax (upon removing the integument at this part, the postscutellum of the mesothorax (*ps*, fig. 2) of the imago is revealed); *met*, the metathorax; *w*, *w'*, the anterior and posterior wing-cases.

2. The thorax of the Crane-fly. The plate, *ps*, between the halteres, corresponding to the posterior wall of the thorax of the Blow-fly, is shown to be mesothoracic, *i. e.* the mesothoracic postscutellum as it is developed beneath the mesothoracic integument of the pupa.
- 3 & 4. The anterior and posterior wing-cases of the pupa of the Crane-fly. The haltere is shown in course of development within the latter.
5. Longitudinal vertical section of the thorax of the Humble-Bee: *ps*, the postscutellum of the mesothorax, to which the muscles, *m*, are attached.
6. The thorax of the same, showing the reduced extent of the metathorax: *col*, the collar; *a*, its posterior angle; *sp*^{*}, spiracle of fifth segment.
- 7 & 8. Figures adopted from Packard, showing the two stages in the development of the pupa of the Humble-Bee. In the latter the thoracico-abdominal constriction is seen to include the fifth segment (*i*) with the thorax: *sp*^{*}, the spiracle of the fifth segment.
9. The thorax of *Liparis salicis*.
10. Longitudinal vertical section of the thorax of *Liparis salicis*: parts the same as in fig. 5.

† Consult *antè*, p. 28.

- Fig. 11. Ditto of *Acrida viridissima*, showing two sets of longitudinal muscles.
12. The marginal disks of the Crane-fly attached to the nerve-centres: *l', l', l'*, those of the legs; *pa*, that of the prothoracic appendage; *w, w'*, those of the wings and halteres.
13. Thorax of *Goerius olens*, showing the dorsal plate of the fifth segment, *i*, attached thereto and separated from the succeeding abdominal ones: *ps'*, the postscutellum of the metathorax.
14. Vertical thoracic muscles of *Æshna grandis*, showing a distinct repetition, 1 2 3 4, 1 2 3 4, in each segment.
15. The subtriangular metaphragma of *Rhizotrogus solstitialis* formed by the postscutellum of the segment, for comparison with the postscutellum in fig. 13.

Instincts and Emotions in Fish.

By FRANCIS DAY, F.L.S.

[Read November 6, 1879.]

DURING the last few years the instincts of brutes have received much attention from biologists, while those of fishes have been generally passed over. Some naturalists have not hesitated to assert that the lives of the finny tribes are destitute of the joys and sorrows generally appertaining to vertebrate animals, attributing to them an almost vegetative existence. In a work lately published in this country, Cuvier's low estimate of their intelligence has again been adopted in its entirety, although during the course of this century much information has accumulated pointing in an opposite direction. Irrespective of this, the ancients must have had a higher opinion of the finny tribes than the authors of the present time, if we are to judge from the attributes they accorded to fish.

But returning to half a century since, we find that Cuvier had no very exalted opinion of the intellect of fishes, considering that among all the vertebrate animals they show the least signs of sensibility, which of course might be expected, as they are the lowest division. Nearly or quite destitute of any voice, with immovable eyes and a fixed osseous face, their physiognomy has no play, their emotions no expression, only capable of hearing the loudest sounds, for, condemned to reside in an empire of silence, they have but small occasion for the sense of hearing. No tear



